Influence of the arrival of *Anoplolepis gracilipes* (Hymenoptera: Formicidae) on the composition of an ant community in a clearing in Gunung Mulu National Park, Sarawak, Malaysia

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ABSTRACT. The yellow crazy ant *Anoplolepis gracilipes* is a common and important invasive ant species in all parts of tropical Asia, including Borneo. We studied the impact of this ant species on the chronological development of an ant community in an artificial clearing at the edge of the alluvial forest in the Gunung Mulu National Park in Sarawak, Malaysia, in the years 2006 to 2009. We used 20 pitfall traps each year to monitor the ant community, in which we found 42 species altogether and 19–23 species in a given year. After the arrival of *A. gracilipes* in 2007 ant community structure changed and diversity (effective number of species and Simpson-diversity) declined, even before species richness itself went down. Ecologically-similar species to *A. gracilipes*, like *Dolichoderus affinis*, were the first species that disappeared. Abiotic factors like the occurrence of irregular flooding events may also have influenced community composition in this clearing. This factor may impact invasive species more heavily than native species, which may be better adapted to these conditions.

Keywords: *Anoplolepis gracilipes*, invasive species, community structure, edge habitat, inundation, Borneo

INTRODUCTION

In the changing world of today, invasive species are of ever-growing importance. Among the one hundred worst invasive species (Lowe *et al.* 2004), with the highest impact on natural ecosystems, five species of ants are listed. These ants are characterised by establishing polygynous super-colonies with the lack of clear colony boundaries (Giraud *et al.* 2002), numerous queens, and low aggression between individuals from physically separated nests (Drescher *et al.* 2007). But against other ant species, they tend to be very aggressive and competitive. These invasive ants can become major agricultural pests by supporting non-native hemipteran vermin (Lester *et al.* 2003) and may cause serious impacts on natural ecosystems by displacing native species (Human & Gordon 1996) or disrupting mutualisms, for example, seed dispersal by myrmecochory (Ness *et al.* 2004). The most important invasive ant species to date are *Linepithema humile*, *Pheidole megacephala, Solenopsis invicta, Wasmannia auropunctata* and *Anoplolepis gracilipes* (McGlynn 1999).

The yellow crazy ant *A. gracilipes* is widespread in many tropical countries (Wetterer 2005), but its origins are unknown. This species was first described from India (Jerdon 1851), but as other species of the genus *Anoplolepis* are exclusively distributed in Africa, an Afrotropical origin is possible. *Anoplolepis gracilipes* can cause severe impacts on ecosystems as evidenced on oceanic islands like the Seychelles (Gerlach 2004) and Christmas Island (Abbott 2005). On

Christmas Island, *A. gracilipes* caused heavy impact on the island's forest ecosystem by killing large numbers of a keystone species, the endemic land crab *Gecarcoidea natalis* (O'Dowd *et al.* 2003); these crustaceans consumed large amounts of leaf litter, seeds and seedlings which resulted in the creation of an open understorey in the island's forests. The crabs' demise changed the forest structure drastically, since litter accumulated and a dense understorey developed. Native trees were weakened by invasive trophobionts which were attended by *A. gracilipes* (Abbott & Green 2007).

    A. gracilipes is widespread in many areas of Southeast Asia (e.g., Bickel & Watanasit 2005; Bos *et al.* 2008). On Borneo it is a very common species, which is mainly distributed in modified habitats (Drescher *et al.* 2007) like oil palm plantations (Pfeiffer *et al.* 2008), forest edges and secondary or disturbed forests, where it interacts with native ants. Several studies in Southeast Asia have been conducted to assess the impact of *A. gracilipes,* by comparing invaded habitats with unoccupied ones, and most of these studies used different areas to compare ant communities (Bos *et al.* 2008).

    In the present study, we used the rare opportunity to examine the effect of invasive ants by noting changes in ant community structure that accompanied the arrival of *A. gracilipes* in the middle of a study on ant communities in an open edge habitat in Borneo.

MATERIALS AND METHODS

Study sites

This study was conducted in Gunung Mulu National Park (NP) in Sarawak (Malaysia) on Borneo. The climate in this 528 km² area is wet-tropical, with mean temperatures in the lowlands of about 26°C and yearly rainfall of 4,000–5,000 mm (Sarawak Weather Service, pers. comm., 2003–2006) In this area, we conducted our study in a 5 to 10 ha large clearing at the Park headquarters (4°03′33″ N, 114°48′49″ E), at the edge of the protected area. Our study site was covered with a species-poor lawn-like vegetation of grass and herbs, kept short by frequent mowing. The site was surrounded by native alluvial forest and adjoined the river bank. Like this forest, the

clearing is irregularly flooded a few times per year. During the study period, the year 2006 had a moderate intensity of flooding events; 2007 had only a few flooding events with low intensity; in 2008, the area was flooded several times very intensively; while 2009 was quite a dry year with no notable flooding events (E. McArthur, research officer Gunung Mulu NP, pers. comm.).

Sampling

We collected samples once a year for a period of four years from 2006 to 2009 (on 11–13 October 2006, 11–13 October 2007, 24–26 November 2008 and 8–10 November 2009). Each time, we placed a transect line of 20 Barber traps in the clearing. The distance between each trap was about 20 m. Each trap was filled with a saturated saltwater solution and detergent. We covered each trap with a plastic cup as rain protection. After 48 hours, we emptied the traps and the content was preserved in 70% ethanol for later identification.

Ant species identification

Identification of ant genera was performed using Bolton (1994) and with a Leica stereo microscope MZ 16. From all species found in this study, we kept voucher specimens that are deposited at the "Antbase.net collection" of the University of Ulm (ABNC), with Automontage© photographs of most species being available via http://www.antbase.net. We classified non-native ant species as invasive, tramp or alien species according to the literature (Passera 1994; McGlynn 1999; Holway 2002).

Statistical analyses

For all forest types, we calculated species rarefaction curves with software package EstimateS 8.2 (Colwell 2009) and by a sample-based rarefaction approach (Gotelli & Colwell 2001). All ants of one (morpho-) species, which were found in one trap, were counted as one species occurrence (SOC), whereas a sample comprised all species collected in one trap. We applied the Mao Tau rarefaction to plot the sample-based rarefaction curves with the number of SOCs on the x-axis (Gotelli & Colwell 2001).

We optimised the estimation of species richness by choosing the optimal estimator with a method suggested by Brose & Martinez (2004); therefore, we: (1) estimated species richness based on all samples by a range of estimators (ACE, ICE, Chao1, Chao2, Jackknife 1, Jackknife 2, Bootstrap, MMMean); (2) calculated the estimated mean of sample coverage; (3) chose the most accurate estimator for sample coverage according to the tables provided by Brose & Martinez (2004) and (4) estimated species richness with this estimator and with the maximum number of SOCs per forest type.

As a measure of "true diversity" (Jost 2006), we used the effective number of species (D), which was calculated from Shannon entropy as given by the Shannon diversity index (H), according to the formula of Jost (2006): D = exp (H). The effective species number equals species richness for the case that all species of a sample have the same frequency. Basic calculation of diversity indices was performed with EstimateS at a common sample size of 80 SOCs for all four years. As a commonly used index, we further calculated Simpson diversity. For the calculation of beta diversity between the four years, we used the abundance-based Chao-Jaccard index which calculates the probability that two randomly chosen SOCs, one from each of two years, both belong to species found in both years (but not necessarily to the same shared species). As this index is quite robust to incomplete sampling, it is especially suitable for such a community with only moderate sampling coverage. This beta-diversity index was also part of EstimateS 8.2 package (Colwell 2009).

To demonstrate the changes within the community between years, we calculated an unconstrained ordination, a non-metric multidimensional scaling (NMDS) which takes most of the variance inherent in the species matrix into account. For this calculation, we used the following settings: distance measurement = Sorensen; maximum number of axes = 6; stability criterion = 0.0100; step length = 0.1; number of runs with real data = 50 and number of runs with randomised data = 249. This calculation was done with the program PCORD Version 5 (McCune & Grace 2002). ANOVAs were calculated with Statistica 6.0 (StatSoft 2003).

RESULTS

In a single year, we found between 19 (2009) and 23 (2006 to 2008) species. During the course of the four years, we altogether recorded 42 species, from seven subfamilies, in the clearing (Table 1); *Tetramorium* and *Monomorium* were the most speciose genera, each with four species. The most common species were *Odontoponera denticulata*, *Monomorium* sp. 6 and *Cardiocondyla tjibodana*, respectively present in 75 percent, 43 percent, and 39 percent of all samples. Of all 42 species, at least four were endemic to Borneo. On the other hand, seven species were non native, one being *A. gracilipes*. This species was recorded in all three years from 2007 to 2009, but was completely absent from the samples in 2006. In the year 2007, this species was recorded in 70 percent of all traps, while in 2008 and 2009 we found *A. gracilipes* in only 10 percent and 15 percent of our samples respectively. The two non-native species *Paratrechina longicornis* and *Tapinoma melanocephalum* were found in all four years, while *Tetramorium simillimum, Tetramorium bicarinatum, Strumigenys rogeri* and *Monomorium floricola* were all recorded in only a single year, with one or two occurrences. As the mean over the four years we collected five species per trap, but species density differed significantly between years; in 2006 and 2009 four species were collected per trap, in 2007 six species, and in 2008 five species (ANOVA; $F_{3,76}$= 5.46; P < 0.0019).

Species accumulation curves showed a medium level of species saturation, as they were still rising (Fig. 1); however, according to the species estimators Jackknife 1 and ICE, we found from 76 percent to 86 percent of all species (Table 2).

The effective number of species declined each year from 2006 (D=16.3) to 2009 (D=13.3) and Simpson-index ranged from 15.81 in 2007 to 12.25 in 2009 (Table 2).

Indices of beta diversity (Chao-Jaccard index) between the four years varied from 0.409, between 2006 and 2009, to 0.834, between 2008 and 2009 (Table 3). Consecutive years proved to be more similar than more distant years, but the year 2007, when species invasion took place, differed greatly from 2006.

Table 1: Abundance of all species found in the clearing. We give information on the number of occurrences in the four years. Under *status*, we note whether a non-native species is classified as tramp (T), alien (A) or invasive (I) species according to the definitions of Passera (1994), McGlynn (1999) and Holway (2002).

Species	2006	2007	2008	2009	Status	Total SOCs
Aenictinae						
Aenictus sp.	0	0	4	0		4
Cerapachyinae						
Cerapachys sp. 12	1	0	1	0		2
Dolichoderinae						
Dolichoderus affinis Emery, 1889	12	5	0	0		17
Iridomyrmex anceps (Roger, 1863)	0	0	0	1		1
Tapinoma melanocephalum (Fabricius, 1793)	3	11	3	6	I, T, A	23
Technomyrmex lisae Forel, 1913	0	1	0	0		1
Ectatomminae						
Gnamptogenys sp.	0	0	0	1		1
Formicinae						
Anoplolepis gracilipes (Smith, 1857)	0	14	2	3	I, T, A	19
C. arrogans (Smith, 1858)	0	0	1	2		3
C. gigas (Latreille, 1802)	0	0	2	1		3
Oecophylla smaragdina (Fabricius, 1775)	3	5	0	7		15
Paratrechina longicornis (Latreille, 1802)	3	10	7	3	I, T, A	23
Nylanderia sp. 8	2	0	0	0		2
Polyrhachis abdominalis Smith, 1858	0	1	0	0		1
Myrmicinae						
Cardiocondyla tjibodana Karavaiev, 1935	5	11	10	5		31
Crematogaster rogenhoferi Mayr, 1879	0	1	3	1		5
Crematogaster sp. 12	6	3	0	0		9
Lophomyrmex bedoti Emery, 1893	2	0	0	0		2
Lophomyrmex longicornis Rigato, 1994	1	4	2	0		7
Monomorium floricola (Jerdon, 1851)	2	0	0	0	T	2
Monomorium sp. 1	0	0	1	1		2
Monomorium sp. 5	4	3	4	4		15
Monomorium sp. 6	4	8	13	10		35
Myrmicaria brunnea Saunders, 1842	2	0	1	0		3
Myrmicinae indet.	1	0	0	0		1

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Table 1 (*continued*)

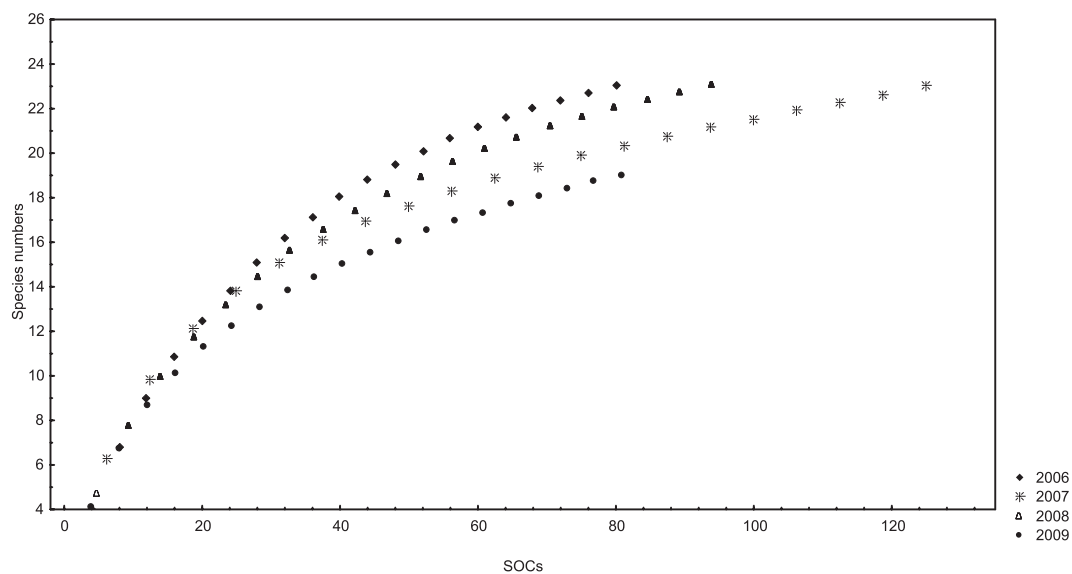| Species	2006	2007	2008	2009	Status	Total SOCs
Oligomyrmex sp. 2	2	3	3	0		8
Pheidole bugi Wheeler, 1919	4	0	0	0		4
Pheidole rabo Forel, 1913	0	8	7	10		25
Pheidologeton affinis (Jerdon, 1851)	3	8	7	7		25
Pyramica aello Bolton, 2000	1	0	0	0		1
Recurvidris kemneri (Wheeler & Wheeler, 1954)	0	2	3	1		6
Strumigenys rogeri Emery, 1890						
Tetramorium (*chepocha-group*) sp.	0	7	0	0		7
Tetramorium bicarinatum (Nylander, 1846)	2	1	0	0	T	3
Tetramorium curtulum Emery, 1895	1	0	0	0		1
Tetramorium simillimum (Smith, 1851)	0	1	0	0	T, A	1
Vollenhovia sp. 2	0	0	0	2		2
Ponerinae						
Diacamma sp. 1	0	0	1	0		1
Leptogenys sp. 1	0	1	2	2		5
Leptogenys sp. 3	0	0	2	0		2
Odontoponera denticulata (Smith, 1858)	15	16	15	14		60
Platythyrea sp. 1	1	0	0	0		1

Fig. 1. Species-abundance curves of the four years of our study; in each year we analysed 20 samples. The rarefaction curves are still rising, indicating only moderate species saturation.

Table 2: Estimated species number and diversity in the four observation years. Given are the species estimator chosen after the method of Brose & Martinez (2004), the estimated species number and the species coverage. Optimal species estimators may change according to sample coverage (e.g., in 2008). We further report two diversity measures, the effective number of species according to the framework of Jost (2006) and the Simpson-index.

Year	2006	2007	2008	2009
Estimator used for calculation	Jackknife 1	Jackknife 1	ICE	Jackknife 1
Collected species number	23	23	23	19
Estimated species number	29	30	27	25
Percentage of species collected	85.67	76.84	86.37	81.61
D (effective number of species)	16.28	15.49	15.49	13.33
Simpson-index	13.62	15.81	13.88	12.35

Table 3: Beta-diversity between the four years. We present Chao-Jaccard index as an inverse diversity measure which calculates the probability that two randomly chosen SOCs, one from each of two years, both belong to species found in both years (but not necessarily to the same shared species). Highest beta diversity measurements (lowest indices) for consecutive years were obtained for the years before and after the species invasion, and highest measures overall for the longest period between samples.

	2006	2007	2008
2007	0.604		
2008	0.469	0.744	
2009	0.409	0.764	0.834

Community structure was analysed by NMDS. The final configuration of the NMDS (final stress 19.65 for a three-dimensional solution) was obtained after 96 tries. Plot scores of the first two axes differed significantly between the four years (Fig. 2), but not the scores of the third axis (ANOVA, axis 1: $F_{3,74} = 16.4$, p < 0.0001, axis 2: $F_{3,74} = 4.2$, p < 0.007, axis 3: $F_{3,74} = 0.5$, p = 0.7). Posthoc tests of the first axis in different years showed that scores of all years after the arrival of *A. gracilipes* differed significantly from scores in the year 2006 when *A. gracilipes* was still absent (HSD, for all three years: p<0.001).

DISCUSSION

With our study, we demonstrate the impact of the arrival of the invasive species *A. gracilipes* on the ant community on a clearing covered by herbs and grass in Gunung Mulu NP. Our results show that the presence of this invasive species leads to a declining Simpson-diversity, even in years when the number of species was still the same. The effective number of species showed the same pattern, declining in each successive survey after the arrival of *A. gracilipes*. The impact of these invasive ants could be underlined by the comparison of the NMDS scores of the community, which revealed a temporal shift in community patterns after the species' invasion, and by the change in
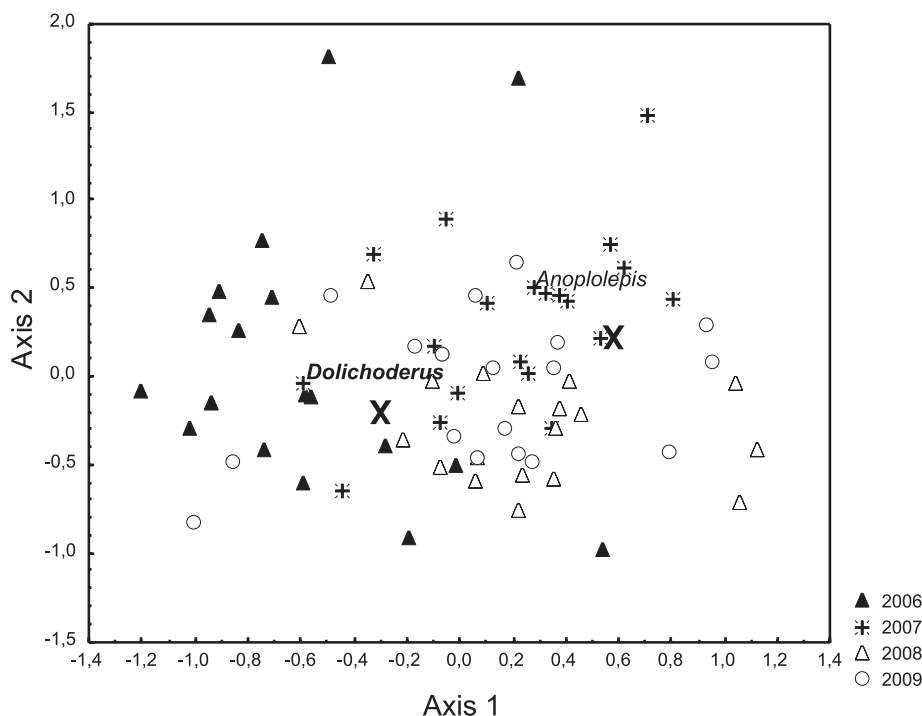
Fig. 2. NMDS Plots of the samples of the four years and the NMDS scores of all 42 species. The scores of *Anoplolepis gracilipes* and *Dolichoderus affinis* are marked by an X. The ant community in 2006 differed significantly from all other years in scores of x- and y- axes.

beta diversity which was especially high in the year of the species invasion.

The impact of *A. gracilipes* on particular ant species can be demonstrated by the example of *Dolichoderus affinis*, a medium-sized dolichoderine ant with opportunistic foraging and trophobiont-tending habits, which is most common in disturbed habitats (Tanaka *et al.* 2007). With these characteristics, *D. affinis* is ecologically similar to *A. gracilipes*. When *A. gracilipes* arrived, *D. affinis* became rarer than the year before, and another year later it seems to have disappeared from this area; *D. affinis* had not recovered when *A. gracilipes* abundance was lower again in the year 2009.

Other non-native ant species seemed to be of lower importance in structuring the community. Two of them, *Paratrechina longicornis* and *Tapinoma melanocephalum*, show a similar distribution to *A. gracilipes*, but they were present before the arrival of *A. gracilipes* in the clearing, so it is difficult to evaluate their impact on community structure. In other areas

of Borneo, *A. gracilipes* seemed to be dominant over *P. longicornis*, for example, around the lab building of the Danum Valley Field Centre about 340 km away, *P. longicornis* almost disappeared after the arrival of *A. gracilipes* (Drescher *et al.* 2007), and similar observations have been made around buildings in rural Hong Kong (John R. Fellowes, pers. comm., 2011). In our study area, we did not observe that *A. gracilipes* outcompeted *P. longicornis*. Four further non-native species, *Tetramorium simillimum*, *T. bicarinatum*, *Strumigenys rogeri* and *Monomorium floricola* were present in only a single year, in low numbers; therefore, these species seemed to have negligible impact on the community.

It is unclear whether *A. gracilipes* entered the area of Mulu by anthropogenic dispersal or by self-dispersal. The species is still spreading in the whole of Borneo; only recently, in 2004, it arrived in the area of the Danum Valley Research Centre by anthropogenic dispersal (Drescher *et al.* 2007). Anthropogenic dispersal is possible only via airplane or boat transport as there is no road

connection from other parts of Borneo to Gunung Mulu NP. But the forested area of this national park adjoins an almost continuous expanse of anthropogenic modified habitats (e.g., secondary forest, scrub vegetation and plantation) that offer suitable conditions for *A. gracilipes* to reach Gunung Mulu NP by self-dispersal. In 2006, before its arrival in the clearing, *A. gracilipes* was already present on the other bank of the Melinau River, which separates the Gunung Mulu NP headquarters from the surrounding scrubland. However, we regularly surveyed the clearing area for ants and other arthropods, and did not observe *A. gracilipes* during our field stays in 2006, or in March/April 2007. The first time we observed this species in the study area was at the beginning of our field stay in August 2007. So we can be sure that the absence of *A. gracilipes* in the clearing in 2006 was no sampling bias.

When we look at the influence of *A. gracilipes,* we must consider that the studied habitat is an anthropogenic modified habitat and heavily disturbed (e.g., by regular mowing). The ant species present there are adapted to disturbance, and some of the species can be found in oil palm plantations (Pfeiffer *et al.* 2008). This already-disturbed ant community was heavily affected by the arrival of the invasive *A. gracilipes.* However, to elucidate the complex changes in ant abundance in detail, we must consider further abiotic effects that affect the ant community on this site. Irregular flooding events one or two times per year were a major abiotic impact to this area and might be expected to impact *A. gracilipes* more than native species, which are adapted to such an environment (Mezger & Pfeiffer 2008).The intensity of these floods might have influenced the abundance of *A. gracilipes* and its potential for further spread; 2007, the year of the arrival of *A. gracilipes*, was a year with only moderately flooding, while the following year, 2008, with a reduced abundance of *A. gracilipes*, showed very heavy flooding events. Although 2009 was again a year with only moderate inundations, *A. gracilipes* could not recover to the frequency of 2007. On the other hand, this species is known to have cyclical variations in abundance even under stable conditions (Wielgoss *et al.* 2010), or drop in numbers after invasion (Haines *et al.* 1994), so there is the potential for further spread in future.

All the non-native species in the clearing seemed to be poorly adapted to flooding events, which are reported to be major forces in structuring ant communities in neotropical alluvial forests (Vasconcelos *et al.* 2010). Frequent inundation may therefore act as a strong environmental filter that supports native species, especially in undisturbed alluvial forest. Regular flooding events may constrain *A. gracilipes* from settling in this forested area; additional constraints include the high diversity of native ants that may prevent species invasions (see Beisner *et al.* 2006), and the complex habitat that might be less suitable for *A. gracilipes*, which prefers disturbed habitat with high insolation. However, a large number of tree-fall gaps caused by recent heavy gales might allow *A. gracilipes* further spread into this forest in the near future.

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